

**FYNBOS CONNECTIVITY
AS A FUNCTION OF DISPERSAL DISTANCE
AND THE IMPLICATIONS
FOR BIRD CONSERVATION
IN THE GREATER CAPE TOWN AREA**

Biological Sciences Honours Project 1

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Kristen Kennedy (KNNKRI001)

Supervised by Professor Graeme Cumming



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FYNBOS CONNECTIVITY AS A FUNCTION OF DISPERSAL DISTANCE AND THE IMPLICATIONS FOR BIRD CONSERVATION IN THE GREATER CAPE TOWN AREA

Connectivity is defined as the degree to which a landscape facilitates an organisms' movement. It is considered a vital element of landscape structure with key implications for metapopulation survival and ecological processes such as pollination. The connectivity of a landscape changes depending on an organisms' ability to move between patches of favourable habitat and this in turn is related to the dispersal ability of the organism. Connectivity thus changes with the scale at which the landscape is viewed; however the relationship between connectivity and dispersal ability is overlooked in many studies. This study looks at the connectivity of two types of fynbos: Highland fynbos (Thicket, Bushland, Bushclumps and High fynbos) which makes up 22.7%, and Lowland fynbos (Shrubland and Low Fynbos) which makes up 28% of the studied extent. These vegetation types are outlined by the National Land Cover Database (NLCD 2000) and analysed as a function of organism dispersal ability in the greater Cape Town area. It is shown that a relationship between dispersal ability and connectivity exists; however the relationship is not linear but sigmoidal with inflection points at 45% connectivity. This raises the question of a connectivity threshold in the Fynbos Biome. Characteristics of the landscape are assessed and it is shown that Fynbos vegetation in the greater Cape Town area is highly fragmented. Fragmentation and habitat loss decrease connectivity and are thus important factors in conservation. In order to simulate the effect of further fragmentation through habitat loss, patches of increasing size were removed and the results put into context for conservation of both the vegetation types and the dispersing organisms dependent on them. The importance of conserving patches of remnant vegetation in order to facilitate organism dispersal is highlighted by this study.

INTRODUCTION

Ability to access sufficient resources in a landscape constitutes the bare minimum for survival of an individual (Fahrig and Merriam 1985). On a larger scale a metapopulations survival depends on the connectivity of the populations of which it is made up (Opdam 1991). Landscape connectivity has been described as a vital element of landscape structure and function and is defined by Taylor *et al.* (1993) as the degree to which the landscape facilitates or impedes movement of an organism. The heterogeneous character of landscapes implies a patchy distribution of resources (Urban *et al.* 1987); the distribution of resources in the landscape has direct consequences for the animals dependent on the patches (Taylor *et al.* 1993). Perhaps the earliest consideration of the importance of patches in a landscape can be seen in the theory of island biogeography (MacArthur and Wilson 1967). In this theory the distance between patches of resources is of great importance for survival of the population.

Work in the last 40 years has built on the basic principles of MacArthur and Wilson's views extending island patches to any favourable resource patch surrounded by inhospitable habitat.

Modelling studies from the 1970s to the 1990s highlighted the importance of animal movement through landscapes, including considerations of the matrix type, the characteristics of corridors between patches and the specific behaviour of individuals in the landscape (reviewed by Tischendorf and Fahrig 2000). Over this period the term 'connectivity' was extensively used in reference to various fields such as genetics, populations, and the physical structure of the landscape; leading to some confusion regarding use of the term. In a landscape perspective connectivity is characterized by two main components: structural and functional connectivity (Kindlmann and Burel 2008). Structural connectivity is of the form referred to by With *et al.* (1997) and defined as "the functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure". In this view the consequence of the matrix type and its effects on an organisms likelihood to express different movement patterns, cross boundaries or face higher mortality risks, is not considered. However landscape connectivity must

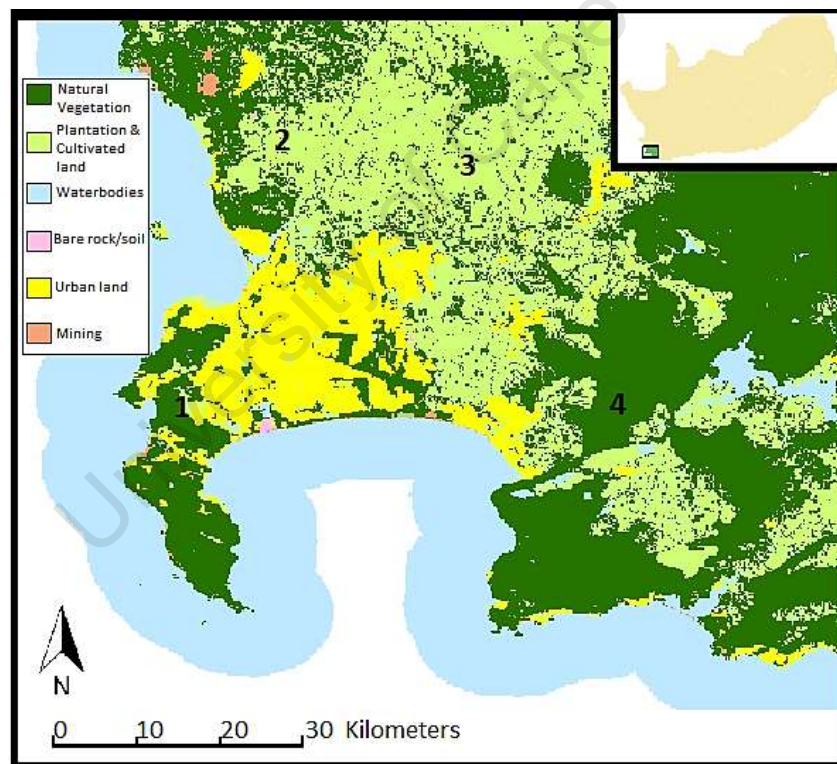


Figure 1. The greater Cape Town region, Western Cape, South Africa, the region is divided into four basic sections for convenience: (1) The Cape Peninsular, (2) The West Coast, (3) The Central Flats, and (4) The Southern Cape Fold Mountains. The region extends from 33° 29'48.55"S; 19° 18'09.84"E in the North East corner to 34° 30'11.8"S; 18° 11'49.37"E in the South West corner. The Map was generated in ArcMap 10 and based on the NLC 2000

include some measure of an animal's movement even if the behavioural responses are not considered. This is the definition of connectivity applied in this paper. Connectivity is not merely the spatial continuity of a habitat across a landscape (page 3 Turner *et al.* 2001); it is also a function of the organisms which interact with the landscape (Keitt *et al.* 1997). In fact, Taylor *et al.* (1993) warns that ignoring movement could have disastrous consequences in the implementation of conservation strategies based on connectivity.

In order to manage and understand the structural connectivity of a landscape some quantification is required. Metrics and landscape indices are common and simple methods for assessing patterns (Kupfer 2012). Connectivity differs from other landscape indices in that it is not based on structure alone but rather on an organism's response to the structure of the landscape. Notably the inclusion of an organism's ability to move through a landscape introduces a common landscape ecology theme to the concept of connectivity, namely the concept of scale. In fragmented landscapes where patches of suitable habitat are isolated by a matrix of inhospitable habitat, an animal's ability to disperse over long distances will determine the degree to which the landscape appears connected (Keitt *et al.* 1997). Distance is especially important in fragmented landscapes as opposed to more continuous landscapes where habitat structure and edge effects play a greater role in species survival (Moilanen and Hanski 2001). In most practical studies it is not feasible to directly measure animal movements (Tishendorf and Farhig 2000); however including a measure of known or approximated dispersal distances to connectivity metrics which include a distance parameter allows for the very necessary link between landscape structure and organism movement to be made (D'Eon *et al.* 2002; Bierwagen 2007).

Table 1. Large conservation regions within the greater Cape Town area

Region	Nature Reserves (NR) (size)
1. Cape Peninsular	Table Mountain National Park (28 700ha)
2. West Coast	Koeberg NR (3 000ha), Table Bay NR (880ha), Blaauwberg NR (1 445ha)
3. Central Flats	False Bay NR (1 200ha), Kenilworth Racecourse Conservation Area (52ha), Rondebosh Common (40ha), Cape Flats NR (32ha), Tygerberg NR (309ha)
4. Southern Cape Fold Mountains	Jonkershoek NR (13 850ha), Hottentots-Holland NR (13 150ha), Steenbras NR (3 000ha), Helderberg NR (402ha), Haweqwa NR (42 160), Kogelberg NR (19 580ha)

As species depend on specific habitat types for survival, loss of available habitat undoubtedly increases the risk of extinction; this is considered one of the most important issues in modern conservation (Wiens 1996). Additionally, organisms which are able to traverse a landscape work to connect ecological processes and offer resilience to the ecosystem by linking functions across the landscape (Olds *et al.* 2012). Antagonised by anthropogenic pressures, loss of habitat tends to increase the level of fragmentation for a given habitat type, increasing the distance between habitat patches (Benton *et al.* 2003). The existence of connectivity thresholds has been discussed (Gardner *et al.* 1987, 2001; Metzger and Décamps 1997). Percolation theory (Stauffer and Aharony 1985) and Graph theory (Urban and Keitt 2001) predict critical points in habitat loss beyond which connectivity goes rapidly to zero (Mönkkönen and Reunanen 1999). Percolation theory predicts a drastic decrease in connectivity when a habitat type makes up less than 45% of the landscape (Gardner *et al.* 1987). Species with dispersal ranges which allow for a landscape which is 45% connected therefore face fewer risks associated with fragmentation. Maintaining connectivity, the inverse of fragmentation, is therefore a priority in conservation management strategies and the construction of habitat stepping stones and corridors to facilitate inter-patch movement is a popular conservation plan the costs and benefits of which are discussed by Simberloff *et al.* (1992).

This study aims to assess the connectivity of a section of landscape in the Western Cape where bird species, the best studied vertebrates of the Fynbos Biome (Siegfried 1979), are dependent on the local flora. Given that fynbos endemics view the landscape as a binary matrix of habitat and non-habitat they serve as ideal candidates for a dispersal based study of the connectivity of fynbos. In this study habitat patches are defined by The National Land-Cover Dataset (2000) (van den Berg *et al.* 2008) and two patches of like habitat are considered connected if they fall within the organisms dispersal distance. Connectivity as perceived by organisms with a range of dispersal capabilities is investigated with particular focus on the state of the landscape according to key fynbos bird species. Connectivity is calculated using the FRAGSTATS CONNECT metric (McGarigal *et al.* 2012). Further, the effects of fragmentation are simulated through removal of patches of increasing size. Finally the implications of these findings are considered with regards to conservation in the region.

METHODS

The overall connectivity of the Fynbos vegetation in a non-fynbos matrix was analysed based on a range of potential dispersal distances for a region of the south Western Cape. Further fragmentation of the landscape was simulated through the removal of increasingly large patches from the region and the change resulting from this loss of habitat was investigated. The implications of both the overall connectivity and the possible future state of the landscape were then considered with respect to their implications for conservation of bird species endemic to the Fynbos Biome.

Landscape Data

The National Land-Cover Dataset (NLCD 2000) was generated from digital Landsat imagery attained from 2000-2001. The original data are in the form of a digital raster with a minimum mapping unit of 2ha and containing 45 land-cover classes which can be simplified into 6 subclasses (Figure 1) (Van den Berg *et al.* 2008). Maps were generated in ArcMap 10 (ESRI 2011). This study covered the southern region of the Western Cape Province of South Africa (33°50'S 18°45'E). The total extent of the studied area is $11.5 \times 10^3 \text{ km}^2$ with land making up $7.0 \times 10^3 \text{ km}^2$ of the total area; all waterbodies were excluded from the landscapes for the analysis (Figure 1).

The study area is composed of four main regions (Figure 1) each containing varying degrees of transformed and natural vegetation. Figure 1 shows a grouping of the classes, simplifying those outlined by the NLCD (2000). The natural vegetation in each of the four sub-regions of the study site is partially protected by nature reserves, of which the larger ones are outlined in Table 1. The dominant natural vegetation is fynbos with some Afromontane forest; however large expanses of the area have been transformed into urban land, cultivated wine lands and forest plantations. It is estimated that 37% of the original vegetation in the Cape Peninsula (comprising roughly half of this study extent) has been transformed by urbanization and agriculture since the area, originally almost entirely fynbos, was colonised by European settlers in 1652 (Richardson *et al.* 1996). The uniqueness of the Fynbos vegetation type sets it far apart from the remaining vegetation allowing for an

Table 2. Bird species included in this study representing dispersal distance range and habitat type, distance classes were constructed based on ring-recovery data and estimated dispersal ranges

Species	Dispersal Distance (km) (mean±std dev)	Distance class (km)	Fynbos Type	Source
Orange-Breasted Sunbird (<i>Nectarinia violacea</i>)	0.5±3.7	<5	Lowland	A. Lee (unpubl.data)
Victorin's Warbler (<i>Cryptillas victorini</i>)		<5	Highland	A. Lee (pers. comm.)
Cape White-Eye (<i>Zosterops pallidus</i>)		<5	Both	Hockey <i>et al.</i> (2005)
Cape Sugarbird (<i>Promerops cafer</i>)	2.93±10.33	5-15	Lowland	A. Lee (unpubl.data)
Cape Rock-Jumper (<i>Chaetops frenatus</i>)		5-15	Highland	A. Lee (pers. comm.)
Southern Double-Collared Sunbird (<i>Cinnyris chalybeus</i>)	2.3±10.3	5-15	Both	A. Lee (unpubl.data)
Black Harrier (<i>Circus maurus</i>)		15-50	Lowland	R. Simmons (pers.comm.)
Cape Siskin (<i>Crithagra totta</i>)		15-50	Highland	A. Lee (pers. comm.)
Malachite Sunbird (<i>Nectarinia famosa</i>)	10.04±37.04	15-50	Both	A. Lee (unpubl.data)

essentially binary view of the landscape. The NLCD (2000) identifies two fynbos vegetation types: Thicket, Bushland, Bushclumps and High Fynbos – henceforth Highland fynbos; and Shrubland and Low Fynbos – henceforth Lowland fynbos. All other land use types defined by the NLCD (2000) were considered inhospitable to fynbos endemic birds and therefore comprised a matrix of ‘non-fynbos’. Landscape connectivity was assessed for patches of Highland and Lowland fynbos as well as both fynbos types combined. The NLCD (2000) raster image was projected using the Albers Equal Area Project in ArcMap 10 (ESRI 2011) with a cell size of 30m².

FRAGSTATS is a fully automated programme developed to quantify landscape structure; it incorporates a range of landscape metrics which can be calculated at different levels (patch, class, or landscape). General characteristics of the landscape were calculated using the following metrics in FRAGSTATS (McGarigal *et al.* 2012):

- Number of Patches of class i ($NP = n_i$)
- Largest Patch Index ($LPI = \frac{MAX_{j=1}^a(a_{ij})}{A}(100)$) as the percentage of the landscape comprised by the largest patch of class i
- Percentage Landscape ($PLAND = P_i = \frac{\sum_{j=1}^n a_{ij}}{A}$) as the proportion of the landscape occupied by patches of class i .

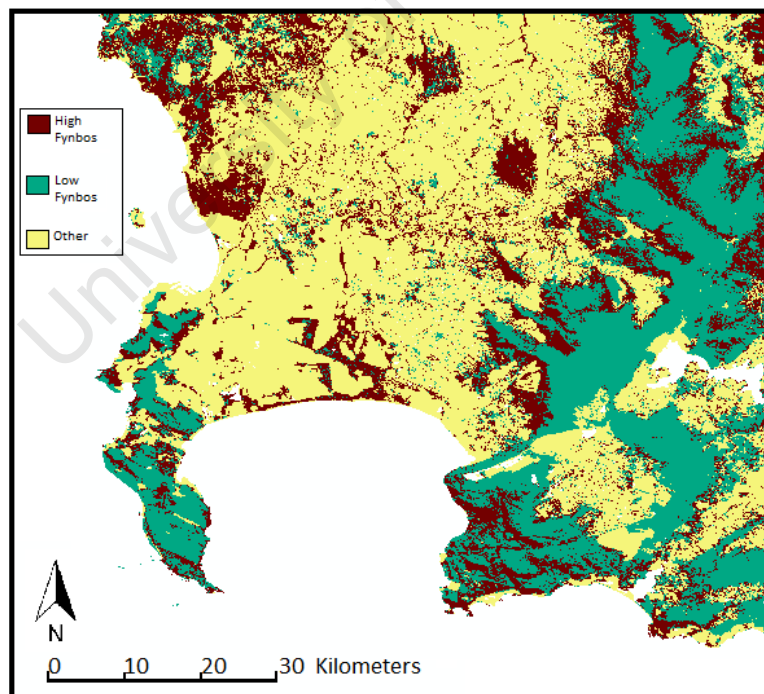


Figure 2. Distribution of Highland and Lowland fynbos over the greater Cape Town Area, the region extends from 33° 29'48.55"S; 19° 18'09.84"E in the North East corner to 34° 30'11.8"S; 18° 11'49.37"E in the South West corner. The Map was generated in ArcMap 10 and based on the NLCD 2000.

Connectivity Metric

The connectivity metric used in this study is the commonly used CONNECT included in FRAGSTATS (McGarigal *et al.* 2012). This metric was appropriate as it includes a simple distance criterion which can be compared to the possible dispersal distance of an animal, thereby fulfilling the criteria of inclusion of an aspect of movement in a connectivity analysis (Moilanen and Nieminen 2002), while excluding more complex forms of modelling such as with incidence function models (Moilanen and Hanski 2001), and percolation models (Gardner *et al.* 1989). Connectivity was calculated for the entire extent of the area over a range of dispersal distances from 0km to 120km in order to include the full range of connectivity (0-100% connected).

CONNECT measures the percentage of habitat patches reachable in one dispersal step from each habitat patch by calculating all possible connections between patches within a distance less than or equal to the specified dispersal distance. The metric is defined as:

$$C_i = \left[\frac{\sum_{j>k}^n C_{ijk}}{\frac{n_i(n_i-1)}{2}} \right] * 100$$

Where $C_{ijk} = 1$ if two patches of type i are connected based on the defined dispersal distance, and $C_{ijk} = 0$ if patches are outside of the dispersal distance; n_i is the number of patches in the landscape of type i . This metric assumes that the disperser does not interact with the non-habitat and is able to cross matrix of any type as long as the next patch is within its dispersal range. This assumption is mostly true for animals able to traverse non-habitat such as some mammals, insects (Bierwagen 2005) and in this case some birds.

CONNECT uses simple movement rules based on an eight-cell neighbourhood rule. It is a useful metric for measuring connectivity in landscapes containing metapopulations and for assessing fragmentation (Pfister 2004; Bierwagen 2007). Connectivity of the landscape was plotted as a function of dispersal distance and a regression was fitted using Least Squares estimation in Statistica (StatSoft 2012).

Species associations

Connectivity was assessed for the unique fynbos vegetation type which is host to six endemic bird species (Barnes 2000) as well as other birds which do not exclusively depend on fynbos but play important roles in ecological processes such as pollination. Nine bird species associated with fynbos were chosen for their representative dispersal distances.

Each species used in this study represents a dispersal range and habitat type (Table 2), classes were constructed based on available data in order to generalise and include species of similar dispersal ability. Using these classes the amount of landscape accessible to each species as a function of dispersal ability was calculated.

Patch Removal

Habitat change has two main components, fragmentation and destruction or loss (Bender *et al.* 1998); however these two components are often linked as destruction of patches leads to further fragmentation of the landscape. In addition smaller patches have a greater likelihood of being lost through transformation. In order to understand the importance of small patches in the landscape all patches smaller than 5ha, 10ha, and 15ha were sequentially removed, this simulates the progression of habitat loss which increases patch isolation (Keitt *et al.* 1997). The connectivity metric is not useful in this regard. As discussed by Moilenan and Hanski (2001); a “deceptive paradox of patchwise connectivity” (Tishendorf and Farhig 2000) exists, whereby removing patches – decreasing the denominator in the connectivity metric – increases the overall connectivity of the landscape as the numerator, - functional joinings between patches – is not similarly affected. This gives the counter-intuitive result that loss of small patches increases the connectivity of the landscape. For this reason a secondary and more simplistic measure of landscape connectivity, the Euclidean Nearest Neighbour distance metric, was used to assess the effects of losing small patches. The ENN distance metric measures the average (\pm standard deviation) shortest distance between patches of the same class (McGarigal *et al.* 2012).

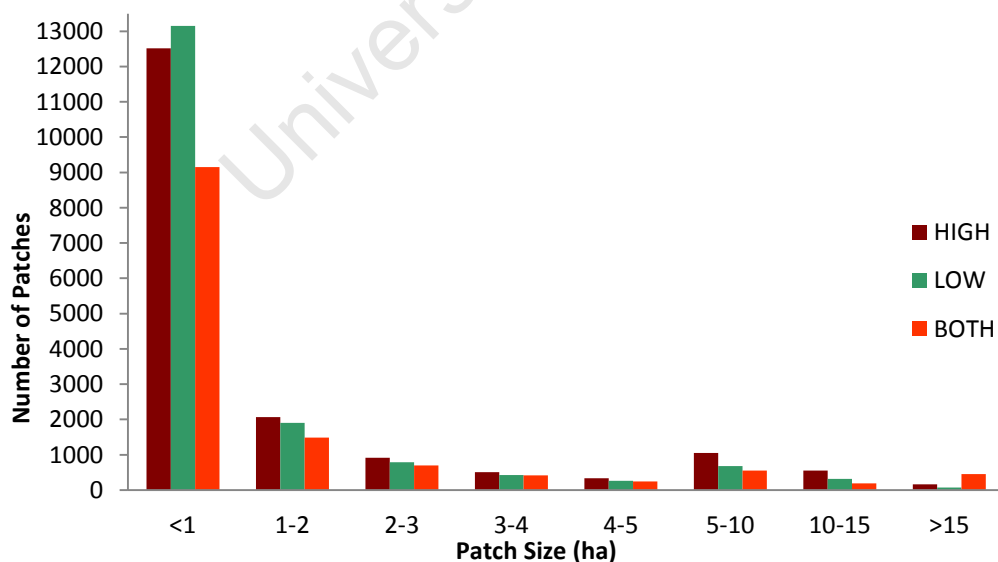


Figure 3. Size distribution of patches of two types of fynbos, Lowland and Highland, and the total if both types are combined into one land class, in the greater Cape Town Area. Classes do not include the upper limit.

RESULTS

Landscapes

The total land area analysed was approximately $7 \times 10^3 \text{ km}^2$ of which 50.7% is fynbos. Lowland fynbos comprises a larger portion of that total with 28% while Highland fynbos covers 22.7% of the land. The areas of greatest fynbos cover co-occur with many of the conservation regions outlined in Table 1 with the greatest patchiness in the Central Flats area (Figure 2) where most urbanisation and agriculture occur (Figure 1).

Lowland fynbos covers a higher proportion of the land and is fragmented into fewer patches (17 044) indicating a more continuous distribution than Highland fynbos (17 606 patches). An ability to survive in both types of fynbos indiscriminately results in a less patchy (13 174) landscape in which almost half of the available land is hospitable. Although Lowland fynbos has fewer patches, a greater proportion of those patches are less than 1ha in area (Figure 3) indicating that this vegetation type is more fragmented at this level than Highland fynbos. However there are more patches of Highland fynbos in all the remaining size classes and the largest patch (indicated by patch density) of Highland fynbos makes up only 2.28% of the total cover of Highland fynbos while the largest patch of Lowland fynbos makes up 12.59% of the Lowland fynbos cover.

Table 3. Linear regressions on the relationship between connectivity and distance for three landscapes composed of fynbos (Highland or Lowland or both) and non-fynbos based on 20 dispersal distances from 1 – 120km and connectivity from 0-100% Confidence Intervals (CI) are given at 95% ($\alpha = 0.05$). The y intercept of the line fitted to the data is given by c and the slope is given by m such that the equation has the form $y = mx + c$, adjusted R^2 values give the proportion of variation accounted for by the linear model

		Est.	Std Error	t-value (df)	P value	Lower 95% CI	Upper 95% CI	R^2
BOTH	c	1,985	3,8290	0,5184 (18)	0,61	-6,059	10,030	0,9243
	m	1,017	0,0666	15,2649 (18)	<0,001	0,877	1,157	
		Est.	Std Error	t-value	P value	Lower 95% CI	Upper 95% CI	R^2
HIGH	c	-1,533	2,8904	-0,5305 (18)	0,60	-7,606	4,539	0,9552
	m	1,013	0,0503	20,1552 (18)	<0,001	0,908	1,120	
		Est.	Std Error	t-value	P value	Lower 95% CI	Upper 95% CI	R^2
LOW	c	-2,217	2,6183	-0,8470 (18)	0,41	-7,719	3,283	0,9625
	m	1,007	0,0456	22,1072 (18)	<0,001	0,912	1,103	

Connectivity

Connectivity of all vegetation types naturally increases as possible dispersal distance increases. The function is nonlinear although fitting a linear regression results in R^2 values greater than 0.9 for all vegetation types (Table 3). A linear model does not account for the exponential behaviour of the graph at low values and the asymptotic nature towards 100% connectivity (Figure 4).

The function which best describes the connectivity relationship is a sigmoidal curve defined by the Boltzmann function with $R^2 = 0.9998$ (Table 4). The curve is of the form:

$$f(x) = A_b - \frac{A_t - A_b}{1 + e^{\frac{-(x-x_0)}{w}}}$$

Where the 'A' parameters denote the bottom and top asymptotes, the curve crosses between these two asymptotic values over a region of x values of width 'w' centred around ' x_0 '. This implies that connectivity changes most drastically over a width 'w' centred around x_0 .

The 'w' parameter allows for the slope of greatest change to be calculated. For all graphs the greatest change in connectivity occurs between 30% and 59% (Figure 4), therefore the curve which

Table 4. Nonlinear regressions on the relationship between connectivity and distance for three landscapes composed of fynbos (Highland or Lowland or both) and non-fynbos based on 20 dispersal distances from 1 – 120km and connectivity from 0-100% Confidence Intervals (CI) are given at 95% ($\alpha = 0.05$), R^2 values give the proportion of variation accounted for by the nonlinear model

		Est.	Std Error	t-value (df)	P value	Lower 95% CI	Upper 95% CI	R^2
BOTH	A_b	-12,229	0,9562	-12,7890 (16)	8,13E-10	-14,256	-10,202	0,9998
	A_t	-125,436	2,0832	-60,2144 (16)	<0,001	-129,852	-121,020	
	x_0	34,555	0,3496	98,8358 (16)	<0,001	33,814	35,296	
	w	15,338	0,2876	53,3280 (16)	<0,001	14,728	15,948	
		Est.	Std Error	t-value (df)	P value	Lower 95% CI	Upper 95% CI	R^2
HIGH	A_b	-11,322	0,9526	-11,8854 (16)	2,36E-09	-13,342	-9,303	0,9998
	A_t	-124,618	2,1725	-57,3613 (16)	<0,001	-129,224	-120,013	
	x_0	40,913	0,3906	104,7442 (16)	<0,001	40,085	41,741	
	w	17,475	0,3640	48,0141 (16)	<0,001	16,703	18,247	
		Est.	Std Error	t-value (df)	P value	Lower 95% CI	Upper 95% CI	R^2
LOW	A_b	-10,548	0,7221	-14,6071 (16)	1,14E-10	-12,079	-9,017	0,9998
	A_t	-123,351	1,6787	-73,4809 (16)	<0,001	-126,910	-119,793	
	x_0	43,026	0,3061	140,5507 (16)	<0,001	42,377	43,675	
	w	18,005	0,2990	60,2191 (16)	<0,001	17,371	18,639	

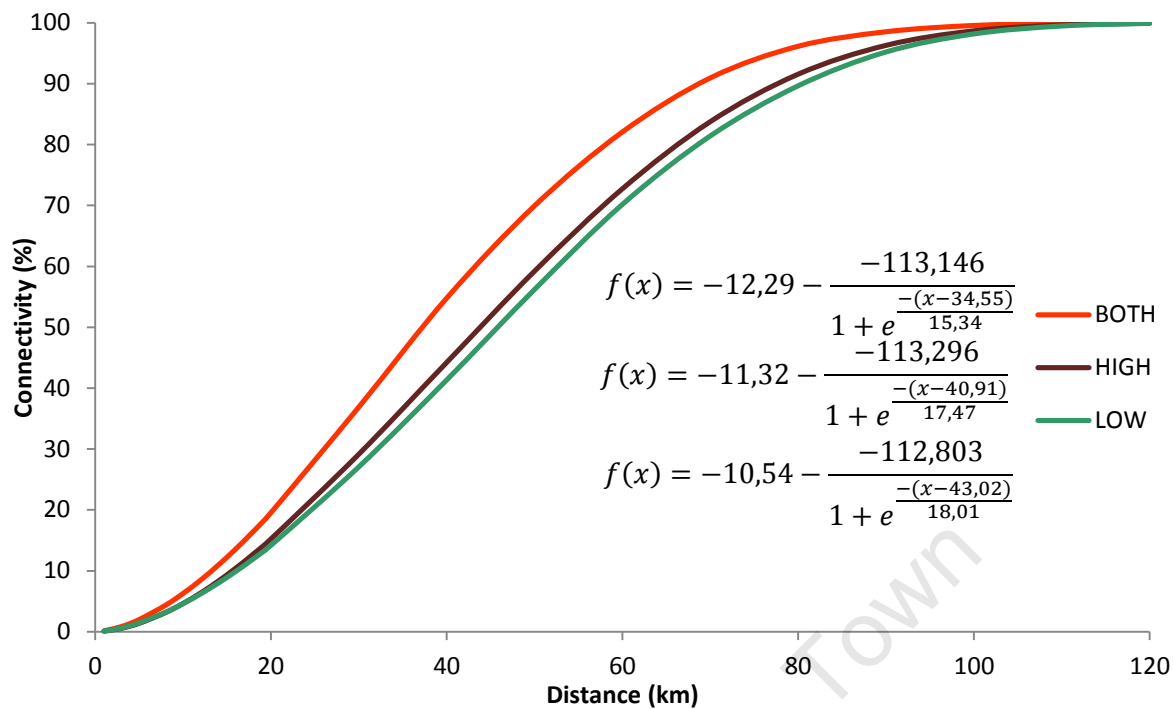


Figure 4. Connectivity (%) against distance (km), where each distance is representative of dispersal ability of an organism in the given landscape (composed of Highland, Lowland or both types of fynbos) analysed over the greater Cape Town Region

makes this change over the largest range of dispersal distances has the lowest slope. Although all three landscapes show similar trends in the relationship between connectivity and dispersal distance, combining both fynbos types results in a more connected landscape (lowest point of inflection, smallest w value). Highland fynbos is more connected than Lowland fynbos with the inflection point occurring at a lower dispersal distance and the range over which the greatest change in connectivity occurs being shorter (17.74km compared to 18.05km) (Table 4 and Figure 4). All inflection points correspond to a connectivity of 45%, as predicted by percolation theory.

Species Associations

Lowland fynbos is the least connected habitat at each scale despite covering a greater area than Highland fynbos. This has implications for the bird species which depend on each of these habitat types independently. For each species, the landscape takes on a different appearance (Table 2 and Figure 5). The current state of the landscape limits the connectivity of patches for all bird species with a dispersal distance less than 40km (45% connectivity in Figure 4). The Black Harrier and other birds with large natal dispersal distances are able to overcome this threshold; however the average foraging distance (15km) of these large birds' results in a landscape which is 9.9% connected. Birds with smaller dispersal ranges have access to fewer habitat patches with generalists dispersing less than 5km perceiving the landscape as 2.0% connected (Cape White Eye Figure 4). Over all dispersal

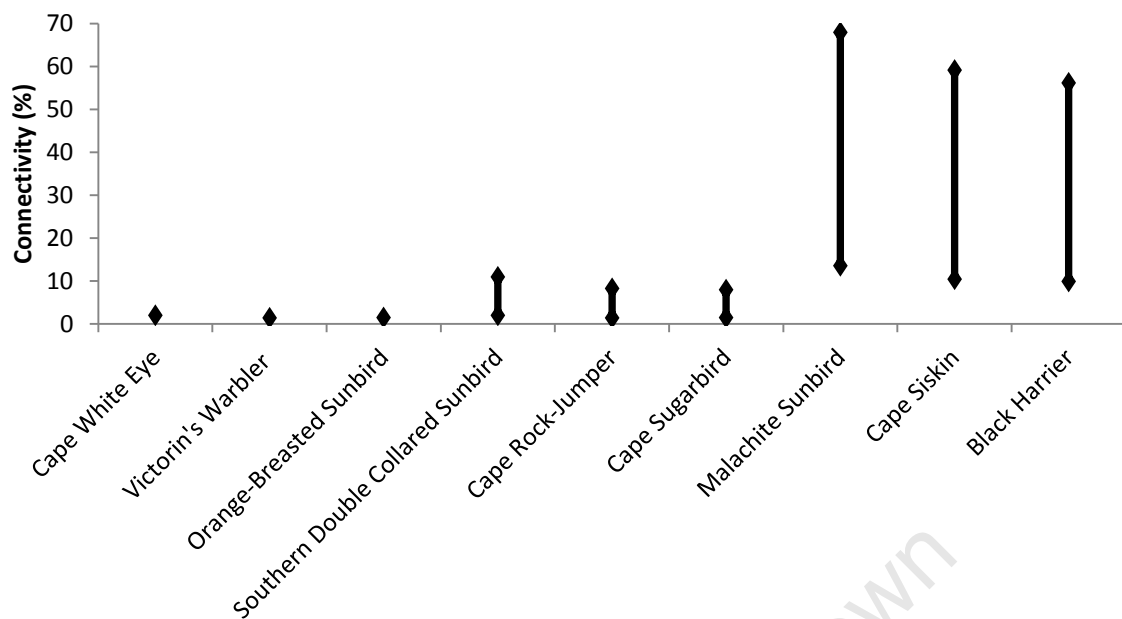


Figure 5. Average range of connectivity of the landscape as perceived by species of fynbos endemic birds with varying dispersal ranges (dispersal distances in Table 2)

distances an ability to survive in both types of fynbos results in a more connected landscape while specificity to Highland or Lowland fynbos results in similarly disconnected landscapes. Species in this study are representative of a range possible average dispersal distances. For example bird species with similar dispersal abilities to that of the Malachite Sunbird may in fact have dispersal ranges anywhere from 15-50 km and therefore may perceive the landscape at any range of connectivity between 14% and 69% (Figure 5).

Patch Removal

When patches are removed from the landscape the landscape is further fragmented and a decrease in connectivity and cover can be seen (Figure 6). The change mostly affects the central Cape Flats area where most small patches are found. Regions that are already protected as outlined in Table 1 are generally made up of larger patches and are therefore mostly unaffected by patch removal. The removal of patches of increasing sizes in the landscape results in the remnant patches being further apart (Figure 7). The average distance between patches, defined as the shortest edge-to-edge distance, increases as the landscape becomes more fragmented through patch loss. In addition the standard deviation around the mean increases as some large patches are unaffected by the loss of small patches and are in some cases proximal. Lowland fynbos sees the largest increase in mean inter-patch distance indicating that small patches play a greater role in facilitating the connectivity of Lowland fynbos. This is enforced by Figure 6 which shows the extreme fragmentation of Lowland fynbos when 15h patches are removed.

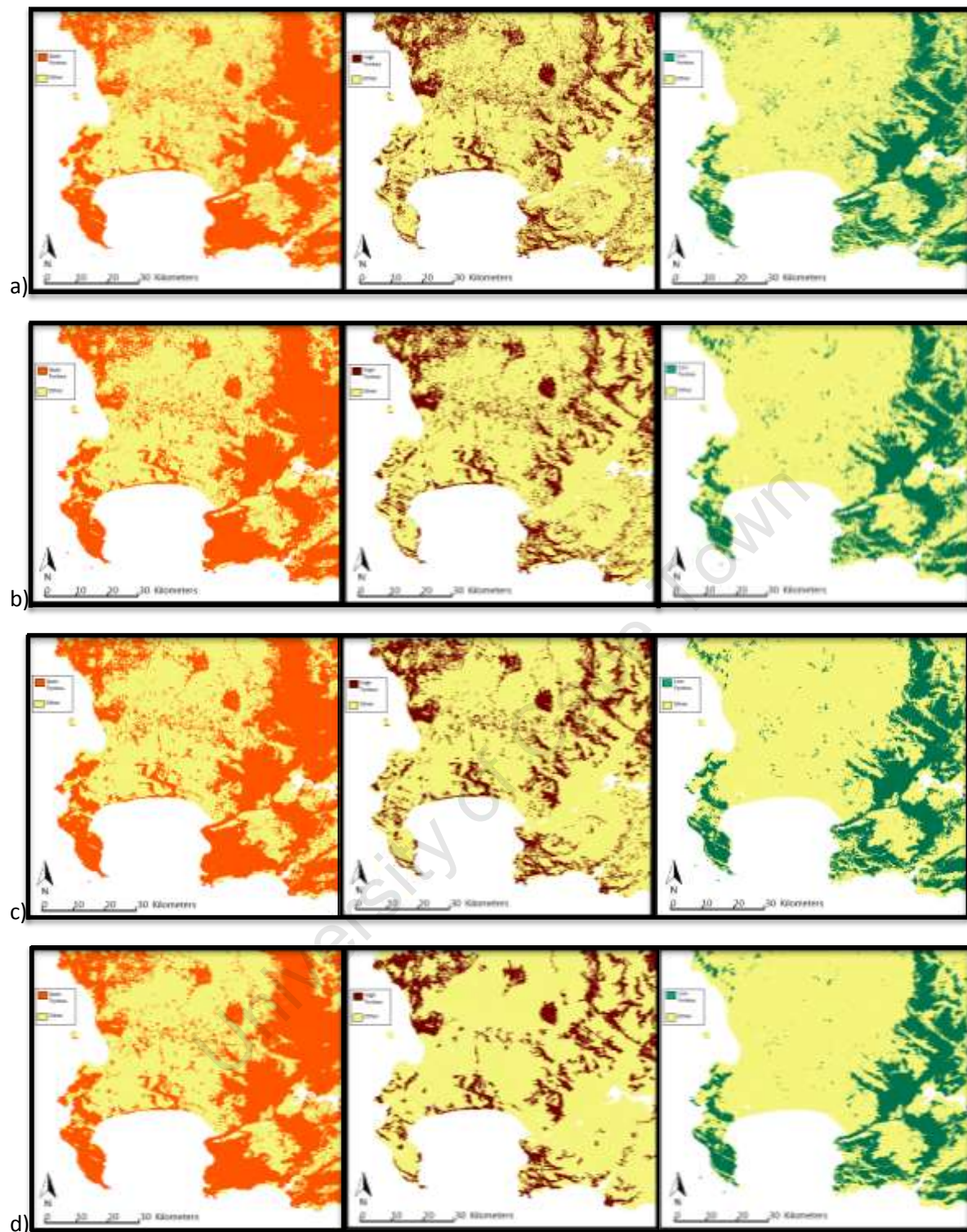


Figure 6. The land cover type representing Both, Highland and Lowland fynbos in the greater Cape Town Area, a) represents the current landscape with no patch removal, b) shows the removal of 5ha patches, c) shows the removal of 10ha patches and d) shows the removal of 15ha patches, over all simulating loss of habitat due to land transformation, Maps are generated in ArcMap and based on land cover classifications of the NLC 2000.

DISCUSSION

The results show that Highland and Lowland Fynbos have a patchy distribution across the greater Cape Town area with some large patches which mostly co-occur with mountain ranges and conservancies. Fynbos, the previously dominant vegetation now covers at most 50.7% of the landscape. Although some fynbos specialists may be indiscriminate, species which depend specifically on a certain type of fynbos (Thicket, Bushland, Bushclumps and High Fynbos or Shrubland and Low Fynbos) exist in a landscape far below predicted connectivity thresholds of 45% land cover. It is evident that the Highland fynbos covers a smaller area than Lowland fynbos, is generally more fragmented (greater number of patches) and has a smaller Largest Patch Index. However, the patches making up the Lowland fynbos are predominantly less than 1 ha in area (74.76% of Lowland fynbos patches are 1ha or less). Lowland fynbos is therefore at greater risk of transformation from anthropogenic pressures than Highland fynbos as it covers more accessible and habitable areas. This explains the large degree of fragmentation in the Central Flats area. These results indicate that the greater Cape Town area has experienced large scale land transformation since colonisation 400 years ago and the two types of fynbos now face different conservation issues based on their prevalence in the landscape.

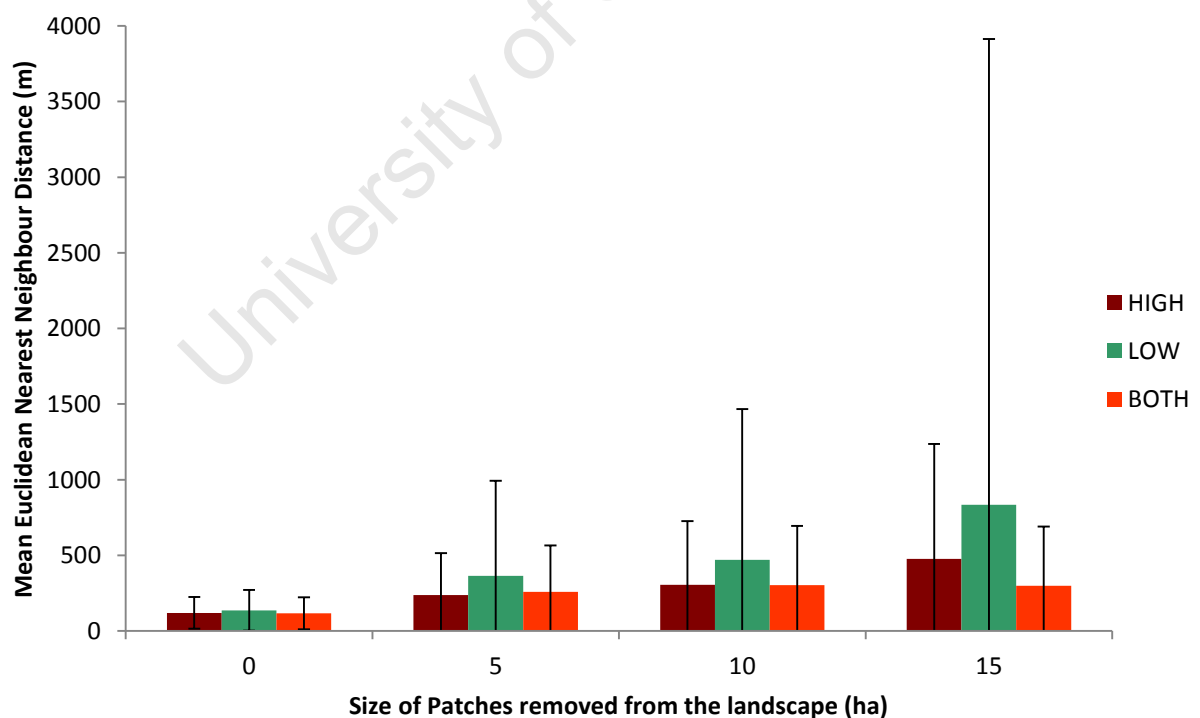


Figure 7. Mean edge-to-edge distance between corresponding patch types in the actual landscape (0 patches removed) and 3 simulated fragmented landscapes, error bars show standard deviation of the mean as calculated by Fragstats on the landscapes generated in ArcMap.

The connectivity analysis shows that landscape connectivity is a function of the dispersal distance of the organism moving across the landscape and that the relationship is sigmoidal (Figure 4). This implies that a point of inflection exists below which connectivity is low (but increases rapidly) and above which connectivity is high (but increases slowly). The relationship was best explained by the Boltzmann equation (Table 4) which has been used to describe connectivity in neural networks (Yang and Shamma 1991; Masulli 1992). Slopes and inflection points could be calculated from the fitted Boltzmann equations which allows for comparisons between the two types of fynbos, however the exponential and asymptotic nature of the curve prevented a perfect fit and, although minimal, systematic over and underestimation occur at these points. For this reason the equation is not recommended for predicting connectivity at various dispersal distances.

Lowland and Highland fynbos have very different distribution patterns over the landscape (Figure 6). Most importantly the connectivity of Lowland fynbos is greatly dependent on the many small patches that allow for connectivity between the large patches located in regions 1 and 2 (Figure 1). Notably the metric used to quantify connectivity in this study is not area weighted, therefore the large area of Lowland fynbos did not affect its low connectivity score across all dispersal distances. Despite appearing less connected than Highland fynbos overall, Lowland fynbos is more connected at dispersal distances below 10 km, a result attributed to the even distribution of small remnant patches over the Central Flats area. In all cases fynbos of the southern Western Cape has low levels of connectivity. Great dispersal ability is required in order to perceive the landscape above the 45% connectivity threshold. Even extremely vagile organisms such as birds require dispersal abilities greater than 35km in a landscape of both fynbos types, and greater than 40-45km in a landscape of Highland or Lowland fynbos. This is outside of the range of many fynbos specific birds (Table 2). The possibility of a connectivity threshold detected by the co-occurrence of inflection points for all three landscapes has interesting implications for the use of this metric as thresholds have typically been found by graph and percolation theory (Keitt *et al.* 1997). In particular Keitt *et al.* (1997) found tipping points at 45km dispersal distance.

These results have important conservation implications for species dependent on Lowland fynbos such as the Orange Breasted Sunbird, Cape Sugarbird and, to a lesser extent, the Black Harrier (Table 2) which may be dependent on the small patches connecting the larger patches of ideal vegetation as stepping stones. In this case conservation management over the flats needs to be focused on ensuring that connectivity is maintained. Patch size is of less importance given that the vegetation type is relatively well represented in large patches over the Peninsula and South Cape Fold Mountains. Connectivity over the central flats therefore demands the most conservation attention. Conserving proximity between patches of like habitat within a species' minimum dispersing ability is therefore of the most importance.

An inverse problem seems to be the case for species dependent on Highland fynbos such as Victorin's Warbler, Cape Rock-Jumper, and the Cape Siskin (Table 2). Movement across the landscape is better facilitated by the distribution of patches, indicated by a higher connectivity at most dispersal distances. Yet patches are generally smaller, introducing risks associated with available minimum ideal habitat area. Management practices in this case should be directed to growing already placed patches and thereby increasing the prevalence of vegetation cover in the landscape. In all cases these birds face threats of habitat loss, not only from land transformation such as urbanisation and agriculture, but from the spread of alien invasive plant species too (Marzluff 2001; Clavero and García-Berthou 2005). Dures and Cumming (2010) conducted a study on the effects of the invasive *Acacia saligna* and found that in the Cape Town area the presence of this tree has a greater effect on avian diversity than urbanised land does.

Bird species such as the Cape White-Eye, Malachite Sunbird and Southern Double-Collared Sunbird (Table 2), are commonly found in the Fynbos Biome but are able to survive over a range of shrubland conditions. They are also well adapted to anthropogenic tree areas such as suburban gardens and plantations. They therefore face far less risk of extinction or metapopulation fragmentation. For these species the landscape is more connected as well as being effectively less binary as they are not completely restricted by the matrix. Species adapted to survive in more than one vegetation type face lower risk of mortality when travelling between patches of ideal habitat. Especially in comparison to birds such as the Orange Breasted Sunbird and the Cape Sugarbird which are reluctant to leave fynbos and are highly dependent on fynbos plants such as *Protea* and *Erica* species (Hockey *et al.* 2005). It is also important to note that the character of the matrix changes throughout the landscape and is not uniformly inhospitable as assumed by this study, in fact it has been shown that the nature of the matrix is important for species response to fragmentation (Antongiovanni and Metzger 2005).

The removal of patches of increasing size showed an interesting possible result of land transformation (Figure 6) with consequences for Highland and Lowland fynbos in the case where small patches are not successfully conserved. Although the same CONNECT metric could not be used on the altered landscapes, as discussed by Tischendorf and Fahrig (2000), the mean nearest neighbour distance worked to describe the effects of the likely scenario where by small patches of vegetation are lost to encroachment or anthropogenic transformation of the land, despite some known weaknesses (Moilanen and Nieminen 2002). The effect of this level of fragmentation results in the possibility of the next nearest neighbouring patch of vegetation occurring outside of a bird's dispersal ability. In the case where the distance to the nearest patch now exceeds the organism's dispersal ability, the population is effectively isolated. Results showed that species dependent on Lowland fynbos would face high risk of population fragmentation if these scenarios are realised. Loss of patches less than 15ha would result in a decrease in patch number of 99.6% but only 14.5% of the available habitat.

Again an inverse problem is created for species dependent on Highland fynbos such that 99.1% of patches are lost as well as 26.9% of the available habitat.

Equally important in light of conservation practices is the quality of habitat in consideration. It is thought that some of the birds with small dispersal abilities such as those in dispersal category 1 (<5km, Table 2) are able to survive in pristine patches as small as 1ha. From this perspective conserving and improving the quality of the small patches that cover the Cape Flats region adds great value to the landscape for the birds dependent on fynbos. As the landscape is, patches of both types of fynbos are on average (\pm std dev) 136.4 m (\pm 134.0m) apart (Figure 7). This should indicate that movement through the landscape is possible by all organisms conforming to the classes in Table 2. If patches of at least 1 ha can be conserved in key locations the populations existing in this landscape could be defended against metapopulation fragmentation. The current representation of habitat in conserved areas may prevent losses of this magnitude. For example, a number of small reserves (less than 10ha) can be found in the Cape Flats area (region 3 Figure 1), due to their size these patches were considered lost by this study but may in reality be saved from urbanisation and encroachment. Importantly loss of habitat due to shifting climates cannot be predicted or accounted for in this context.

The conclusions drawn regarding species associations and connectivity are subject to a few limitations. Of highest ecological importance is the possible mismatch between the classes outlined by the NLCD 2000 (Thicket, Bushland, Bushclumps and High Fynbos and Shrubland and Low Fynbos) and the habitat dependence of bird species. For example, the Cape Sugarbird is described as locally common in mountain fynbos and Shrubland (Hockey *et al.* 2005). The large generalisations of the NLCD therefore do not accurately convey the high level of specificity found in species associated with the Fynbos Biome. It is important to keep in mind that these species are representative of all bird species which exist along a gradient of habitat affinity and a range of dispersal ability. Although the binary nature of the landscape is a major limitation of this study it is not an uncommon method for simplification (D'Eon *et al.* 2002) and may be easily rectified through analysis based on different land class classification and empirical data based on specific species and habitat types of interest.

The figures of habitat loss and fragmentation generated by this investigation of connectivity of the southern Western Cape describe a system where connectivity is greatly affected by the scale at which the landscape is perceived. In addition important points for the conservation of Highland and Lowland Fynbos can be made, namely that Highland fynbos is more connected but less represented than Lowland fynbos which is less connected but more represented in the landscape. The metrics used to make these conclusions should be taken into account in conservation planning for both the vegetation types in question and the dispersing species dependent on them.

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